A PERMINERALISED CUPULATE FRUCTIFICATION FROM QUEENSLAND

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Cupules containing 2-8 ovules are described as *Dawesia cupulata* gen. et sp. nov., a taxon of uncertain affinities. The cupules and single dispersed ovules are embedded in permineralised peat boulders of Jurassic age which occur surficially at Miles but are incorporated in sediments of the Kumbarilla Beds at Chinchilla.☐ *Jurassic, fructification, Dawesia cupulata.*

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Permineralised peat known to the lapidiarists of southeastern Queensland as "forest-floor" is rich in plant material amongst which, leaves, stems and ovules are conspicuous. The preservation of tissues in the peat is poor, except for that of the wood and the ovules, the cell structure of whose integuments is discernible. Abundant impressions of a *Cladophlebis* sp. are also present on some surfaces. Although most ovules are solitary they sometimes occur in clusters which are enclosed in cupules (Figs 1,2). The earliest known collection of a cupule is that of E.O Marks, who early this century, found a specimen in the Chinchilla district. A photograph of the cupule, labelled "Gymnospermous seed capsule" has been published by Hill et al. (1966).

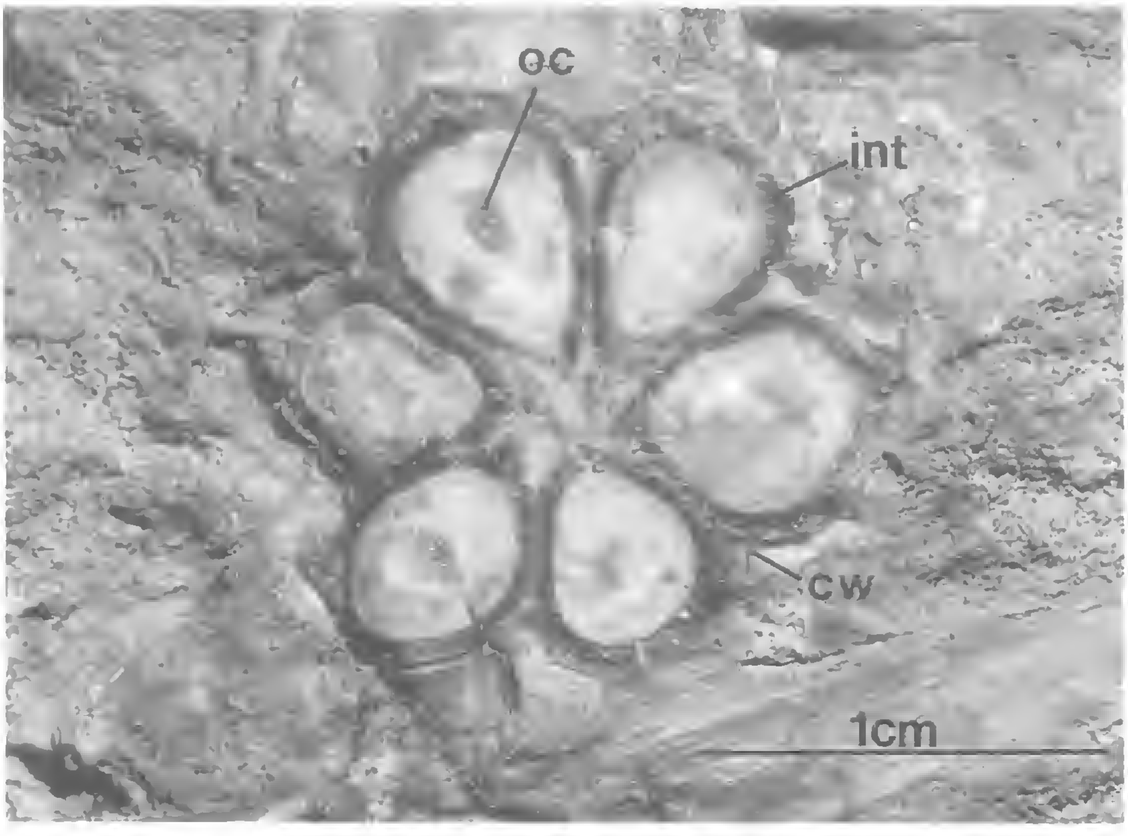

FIG.1. *Dawesia cupulata* gen. et sp. nov., holotype, QMF32157, rosette of ovules, exposed on the surface of a boulder of "forest floor"; collected at Miles: oc, ovule cavity; cw, cupule wall; int, integument.

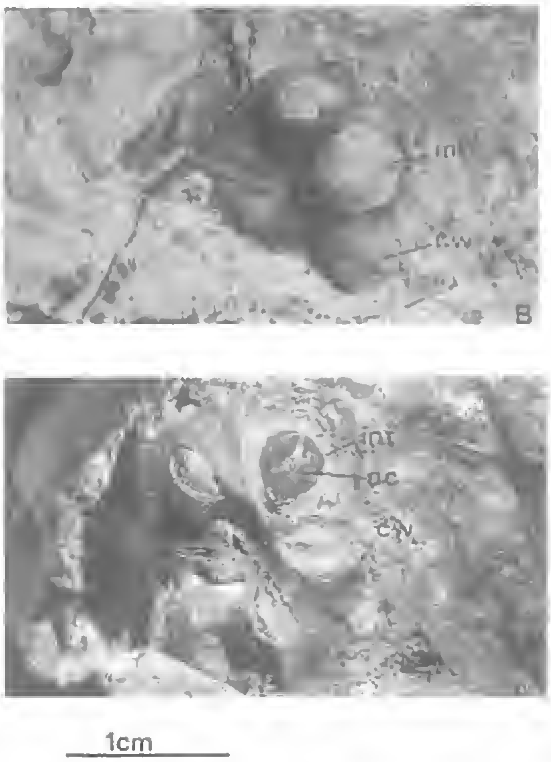

FIG.2. *Dawesia cupulata* gen. et sp. nov. A-B, Cupules of paratypes exposed on the surfaces of two "forest floor" boulders collected from along Rocky Creek near Chinchilla. A, QMF32185. B, QMF32184. Oc, ovule cavity; int, integument; cw, cupule wall; cb, cupule base; o, ovule.

ABBREVIATIONS USED: QM, Queensland Museum; GSQ, Queensland Geological Survey.

STRATIGRAPHY

The source of most "forest floor" specimens is uncertain because all have been collected as surficial boulders from hillsides or stream beds. However, at least some of those boulders which show little evidence of abrasion and have been collected from along the bed of Rocky Creek, Chinchilla almost certainly derive from a lens of "forest floor", incorporated in a single sandstone bed which is exposed in the low cliffs forming the right-bank of the Creek (26°34'S, 150°36' E) 100-200m upstream from the collecting site.

The strata which are exposed in the cliffs are members of the Kumbarilla Beds a series of fine to coarse grained sediments and thin bands of coal, for the most part, laid down in stream, deltaic and lake environments (Reiser, 1971). Lenses of permineralized peat are also present. The Beds are about 600m thick and dip gently to the south. They range in age from Late Middle Jurassic to earliest Cretaceous (Day et al., 1983) or to Upper Cretaceous (Exon, 1976).

The only in situ "forest floor" encountered in this study was a lens about 2m long and about 15cm thick which being incorporated in a sandstone bed that occurs in the upper portion of the Kumbarilla Beds is close to the Jurassic-Cretaceous boundry. None-the-less the *Cladophlebis* leaf impressions associated with the cupules derive from a typically Jurassic taxon (J. Rigby, pers. comm.) thereby confirming the pre-Cretaceous age of the "forest floor". As the ovules in the permineralized peat are not compressed it must have been silicified before being deeply buried. The source of silification is not known but from an examination of thin sections of "forest floor" it is evident that at least two phases of silicification have occurred (A. Cook, pers. comm.).

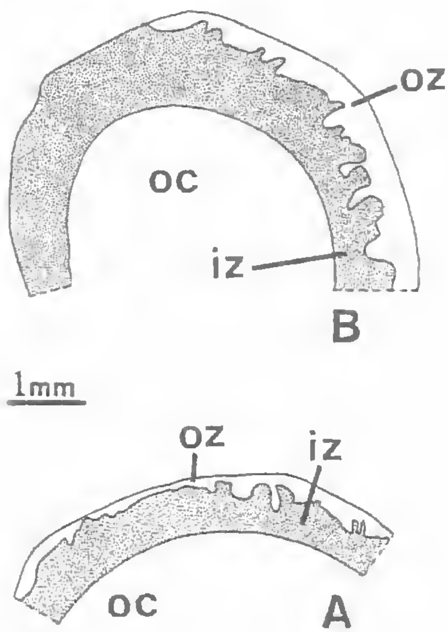

FIG.3. A-B, Integument of *Dawesia cupulata* gen. et sp. nov. A, QMF31911, upper portion of integument of central ovule in Fig.10C viewed in reflected light. B, QMF32160, portion of an integument viewed in transmitted light. oz, outer zone; iz, inner zone; oc, ovule cavity.

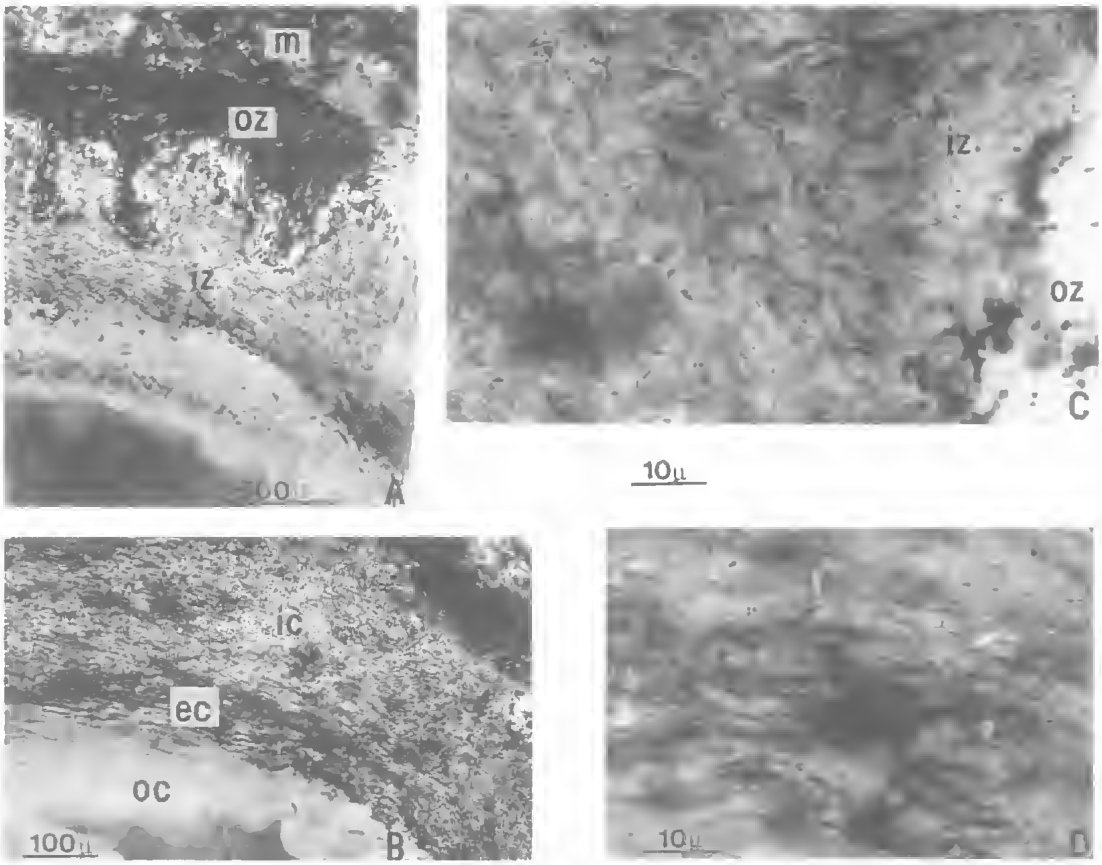

FIG. 4. *Dawesia cupulata* gen. et sp. nov. A-D, QMF32161, transverse sections of integument, viewed in transmitted light. A, Integument and ovule cavity. B, Inner zone of integument and ovule cavity. C, Isodiametric cells of integument. D, elongated cells of integument close to ovule cavity: m, investing matrix: oz, outer zone; iz, inner zone; oc, ovule cavity filled with chalcedony; ec, elongated cells; ic, isodiametric cells.

SYSTEMATIC PALAEOBOTANY

Division INCERTAE SEDIS
Form Order DAWESIALES ord. nov.
Form Family DAWESIACEAE fam. nov.
Dawesia gen. nov.

DIAGNOSIS
As for the only presently known species.

TYPE SPECIES
Dawesia cupulata sp. nov.

DIAGNOSIS
Ovuliferous organs consisting of cupules, each bearing 2-8 turbinate ovules on its inner surface, micropyle not extended and the integument membranous throughout, lacking vascular tissue and resin bodies; cupules pedicellate and possibly occuring in pairs.

ETYMOLOGY
For Graham Wallace Dawes, the collector of QMF32157. Latin *cupulata*, like a cup.

Dawesia cupulata sp.nov.
Figs 1-10

DIAGNOSIS
Cupule hemispherical, c. 16mm in diameter, the outer surface ribbed; ovules turbinate, 8-9mm long and 7mm in diameter.

MATERIAL EXAMINED
HOLOTYPE: QMF32157, Miles, Queensland 26°35'S, 150°16'E.

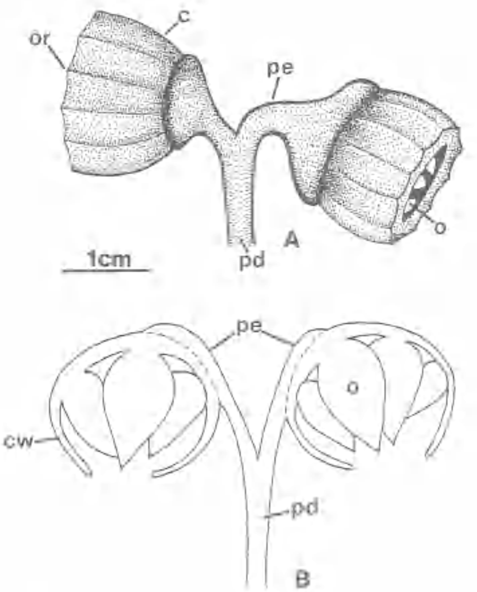

FIG.5. *Dawesia cupulata* gen. et sp. nov. A, Reconstruction of a pair of cupules. B, Diagrammatic longitudinal section of cupule pair illustrated in Fig 5A. Though illustrated as occuring in pairs the cupules may be solitary. C, cupule; cw, cupule wall; o, ovule; pe, pedicel; pd, peduncle; or, ornamental rib.

PARATYPES: QMF32156, QMF31911, GSQF141; Chinchilla, Queensland 26°134'S,150°36'E.

DESCRIPTION

Ovule morphology. Mature ovules, as recognised by their having been shed from the cupule, are turbinate and 8-9mm long, with maximum width c.7mm one third of the distance from the broad chalazal to the narrow micropylar end. The radial symmetry of the ovules may be modified by compression resulting from contact with adjacent ovules. The ovules arise from the basal region of the inner surface of the cupule and they lack micropylar beaks.

The integument is unvascularised and has no internal glands. It is about 1mm thick and is usually differentiated into two zones which are separated by an irregular boundary. The outer and usually narrower of the two zones, when present, is light- to pale-brown whereas the inner is brown to dark-brown. The zones are evident in both transverse (Fig. 10A-B) and longitudinal (Fig. 10C) sections and are clearly discernable in both transmitted (Fig. 4A) and reflected light (Fig. 10A-C). Although the boundary between the zones is quite definite it has no regular pattern and is not associated with any constant differences in cell-type. It is apparently an artifact that arose during the process of mineralization. Support for this interpretation of the origin of the zonation is afforded by the inconstancy of the widths of the two zones and the complete absence from some integuments, or parts thereof, of the pale outer zone (Fig. 3B).

The cells of the integument are either straight-walled and isodiametric with diameters of 25-35μm (Fig. 4C) or are elongated with slightly curved walls (Fig. 4B,D). The elongated cells, which may be up to three times longer than broad with diameters similar to those of the isodiametric cells, occur towards the inner side or the base of the integument. The long axes of the elongated cells have no consistent orientation but are mostly disposed obliquely or at right angles to the long axis of the ovule. The cells lining the micropylar canal do not differ markedly from the adjacent cells of the integument.

The shapes of the epidermal cells of the integument are unclear and no stomates have been observed. Furthermore, no megaspores, megaspore walls or gametophytes have been observed. The ovule cavities are filled completely with chalcedony.

Cupules. The ovules are borne in pedicellate cupules. The pedicels are possibly paired and are attached laterally close to the bases of the cupules (Figs 5A-B). As seen in vertical section the walls of the cupule completely embrace the ovules and are thinner on their sides than bases. Each cupule contains up to eight ovules which arise near to the base from its inner surface (Fig. 5B). A fully mature 6-8 ovuled cupule has a diameter of about 16mm. The upper surface of the cupule is ribbed (Figs 5A,10A,B).

The epidermal cells of the outer surface of the cupule illustrated in Fig. 2B are of two types. The majority are square to rectangular in outline with slightly curved anticlinal walls. As seen from above the surfaces of the epidermal cells are pitted or finely grooved. The remaining cells are arranged in rings of 5-6 and disposed around apertures which presumably lead to sunken stomates (Fig. 6).

The above description of the cupule morphology derives from three sources.

1. *Partially exposed ovules.* The beautiful rosette of ovules which first directed attention to *Dawesia cupulata* is exposed on the surface of a boulder (Fig. 1). The cupule which is here re-

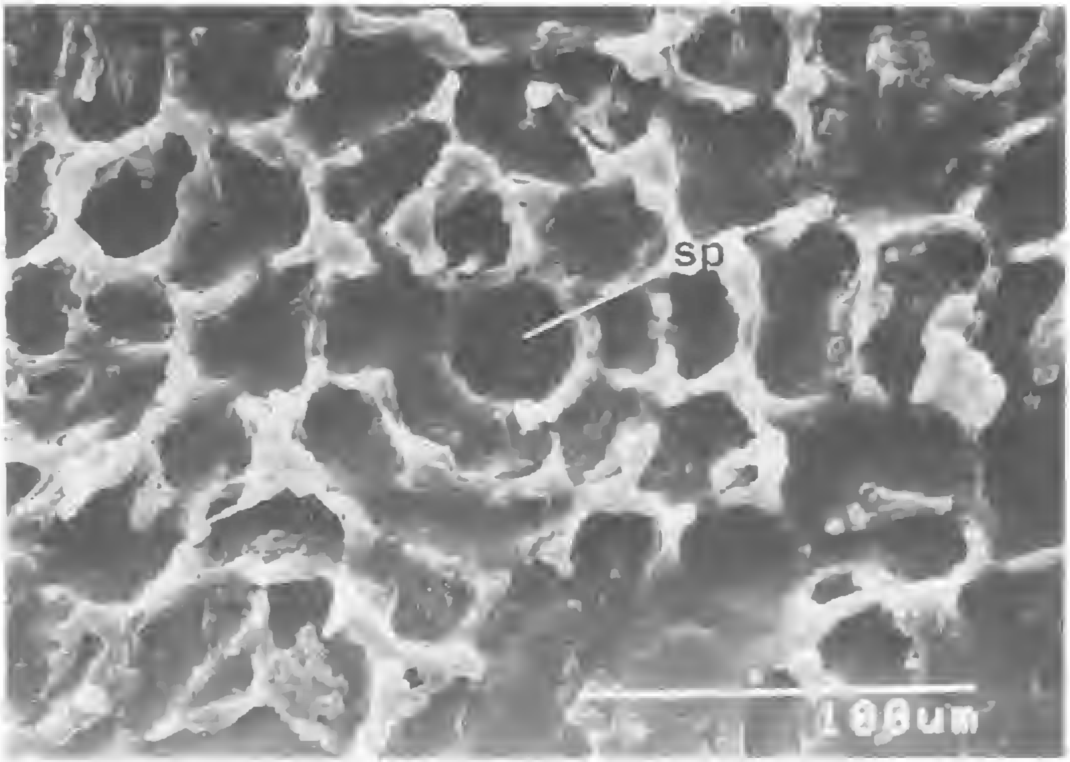

FIG. 6. *Dawesia cupulata* gen. et sp. nov. Epidermal cells as revealed in an electron micrograph of latex mould taken from the central area of the outer surface of the cupule illustrated in Fig. 2B: sp, stomatal pore.

vealed in transverse section is represented only by fragments of its wall. There is no clear indication of a central axis at the centre of the rosette suggesting the cupule is not peltate, as is confirmed by longitudinal sections. The two other clusters of ovules (Fig. 2) are revealed through the eroded bases of their cupules whose slight assymmetry is ascribed to the lateral attachment of their pedicels.

2. *Parallel sections.* The outlines of a partial cupule (Figs 7,8) and its enclosed ovules are exposed on the four surfaces of two adjacent slabs, cut from the same boulder as that with the rosette on its surface.

Using a common margin of the slabs as a reference line and allowing both for the differences in slab thickness and the width of the saw-cut a section of the cupule was constructed as it would appear at right angles to the exposed surfaces (Fig. 9). The dispositions of the ovules in this reconstructed section confirm they were borne in a cupule. The lack of continuity of the right hand wall of the cupule and the separation of the ovules suggests that considerable decomposition had taken place before preservation was achieved.

3. *Single sections.* Three additional cupule outlines are available. Using ovule shape as the determining criterion two of the sections are regarded as transverse and the third as longitudinal.

(a) *Transverse sections.* Because the outlines of the ovules are circular to elliptical with widths near to the maximum observed it is assumed both cupules have been cut across transversely and near to their bases (Figs 10A-B,11A-B).

The cupule walls are thin (Figs 10B,11B) and their outer surfaces are ornamented with small projections which are interpreteted as superficial ridges seen in section.

(b) *Longitudinal section.* Because the outlines of its ovules are turbinate it is assumed the cupule has been cut longitudinally an opinion supported by the outline of the central of the three ovules whose integument is uniformly wide except where interrupted by the micropylar canal (Figs 10C,11C). As expected where ovules are arranged in a circle the micropylar canals of the adjacent ovules are not visible on the exposed surface but can be seen through their integuments by focusing down into the almost transparent investing matrix.

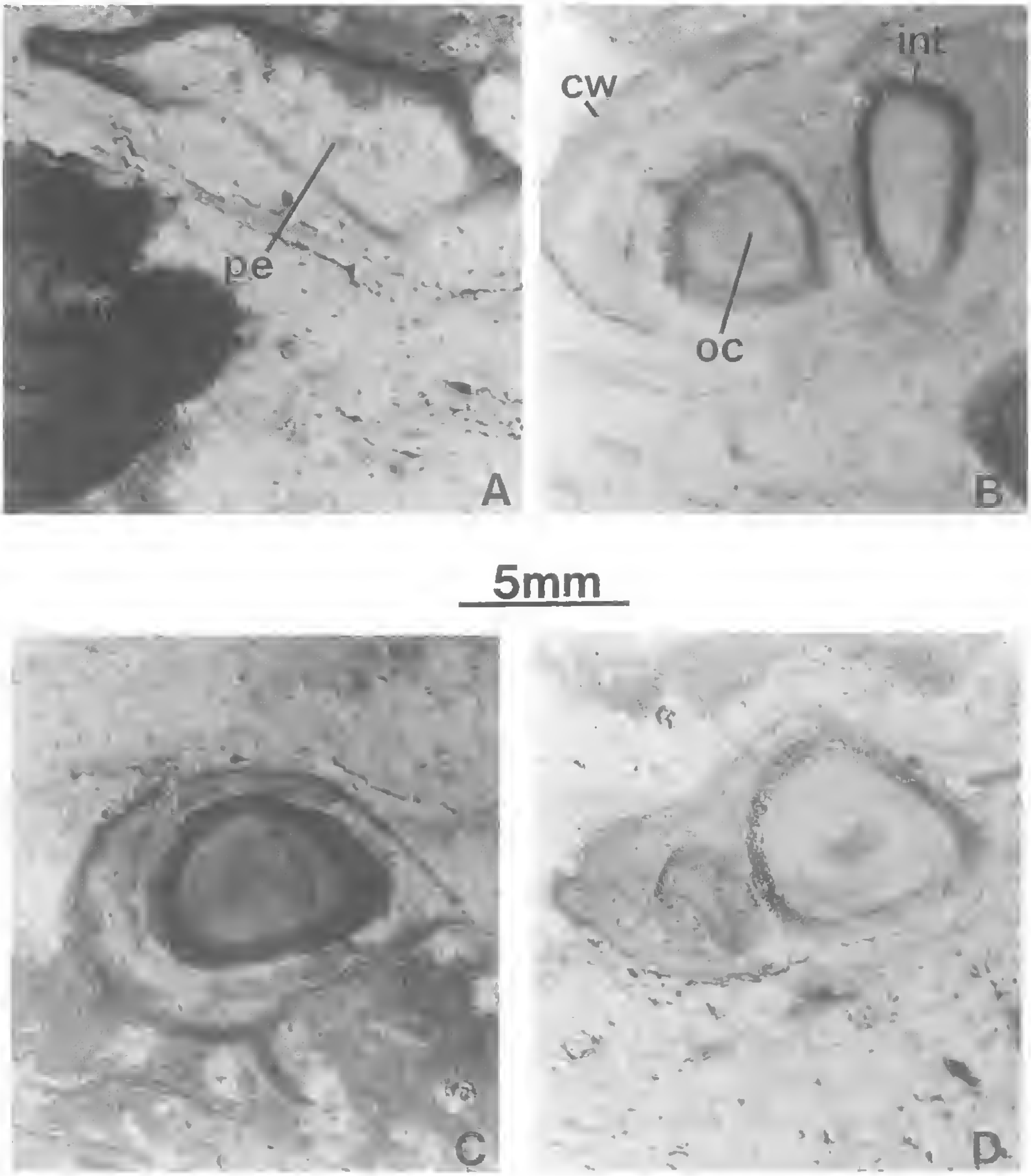

FIG. 7 *Dawesia cupulata* gen. et sp. nov. A-D, sections of an incomplete cupule of as exposed on the four planes resulting from the cutting of two parallel slabs from the boulder that includes the holotype. A-B, QMF32159a. C-D, QMF32159b: pe, pedicel; int, integument; oc, ovule cavity; cw, cupule wall.

The cupule wall completely embraces the ovules and is quite thin except at the base where it is attached to the pedicel. Unfortunately no tissues are preserved in this area but it appears that at least part of the apparent thickness of the cupule base may result from separation of the outer epidermis from the surface of the cupule. In the right-hand side of this space a small rock fragment has been incorporated.

In this plane of section no surface ornament is present as would follow if the projections seen in the tranverse sections are those of superficial

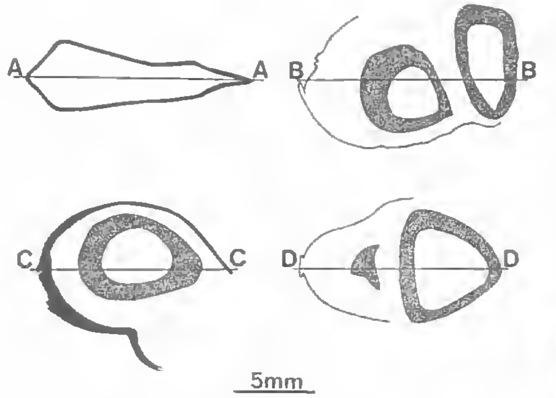

FIG. 8. A-D. As for Fig. 7. A, Pedicel of cupule. B-D, transverse sections of cupule.

ornamental ridges radiating from the base of the cupule.

Neither of the elliptical structures close to the apex of the ovule on the right-hand side of the cupule is regarded as associated with that structure.

The two cupules of which one is exposed in longitudinal section (Fig. 10C) and the other in transverse section (Fig. 10B) occur in close proximity on the facing surfaces produced by a single saw-cut. Though no organic connection between the two cupules has been established it has been assumed their close association indicates that the cupules occur in pairs. The manner of arrangement of these pairs into infructescences is not known.

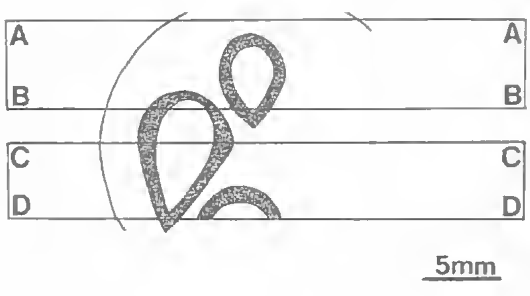

FIG. 9. *Dawesia cupulata* gen. et sp. nov., longitudinal section of a cupule reconstructed from the four transects marked on the sections illustrated in Fig. 8.

DISCUSSION

The cupules of *Dawesia cupulata* are of particular interest for being permineralised and uncrushed their gross morphology can be reconstructed with reasonable certainty. None-the-less, due to their poor state of preservation and lack of associated foliage the taxonomic affinities of the genus are unclear. The protection of ovules within a cupule is a feature that has evolved on several occasions and so is of little value for defining higher level taxa. Therefore, in

FIG. 10. *Dawesia cupulata* gen. et sp. nov. A-C, sections exposed on the surfaces of slabs cut from the boulder that includes the holotype. A, QMF32186, transverse section of a 2-ovulate cupule. B, QMF32156, transverse section of a >3-ovulate cupule.C, QMF31911, longitudinal section of >3-ovulate cupule with the central ovule cut in the median

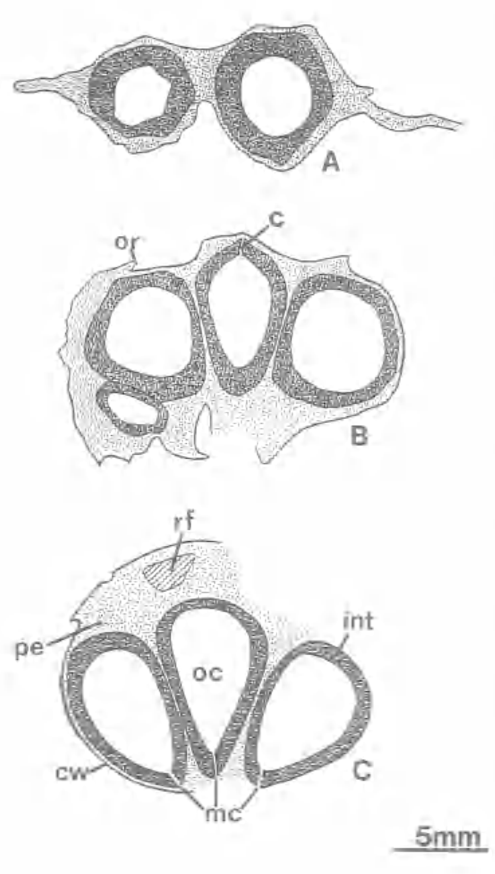

FIG. 11. *Dawesia cupulata* gen. et sp. nov. As for Fig. 10. cw, cupule wall; int, integument; mc, micropylar canal; oc, ovule cavity; or, ornamental rib; pe,pedicel.

order to determine the taxonomic affinities of *Dawesia* particular attention must be paid to the structure of its ovules. In particular the vascularisation, presence of sclerenchymatous bands and the occurence of secretory tissue are important diagnostic features.

Although there is some differentiation of cells within the integument the cells are all parenchymatous and secretory tissue is lacking. It is assumed that the integumentary cells of *Dawesia cupulata* are primarilly thin walled and that this condition does not result from the destruction, during fossilisation, of otherwise thick cell walls thereby leaving only their middle lamellae. The destruction of such thick walled cells has been reported by Srivistava (1946) to have occurred in the integuments of some *Carnoconites* (Form Genus for the ovules of *Pentoxylon*) specimens he investigated. The single integument of *Dawesia* ovules and its lack of differentiation into three layers, an outer and inner composed of parenchyma with a fibrous middle layer, reduces considerably the taxa to which the genus may be related.

Thus the integument being single rather than double disqualifies *Dawesia* from membership of the Cordaitales, Gnetales and Taxales (Coulter & Chamberlain, 1917) as well as the primitive angiosperms (Denffer et al., 1980). Furthermore, lack of differentiation of the integument excludes *Dawesia* from membership of the Pinophyta, Cycadophyta, Ginkgophyta, Bennettitales (Coulter & Chamberlain, 1917), Caytoniales and Pentoxylales (Sporne 1974).

Attention is therefore drawn to the Mesozoic "seed ferns" , Peltaspermales, Corystospermales and Petriellales as possible relatives of *Dawesia* for all these Orders have undifferentiated, unitegmic ovules. Furthermore, ovulate fructifications of both Peltaspermales (Holmes, 1982) and Corystospermales (Holmes & Ash, 1979; Holmes 1982 & 1987; Playford et al., 1982; Retallack, 1980; Shirley, 1898) have been reported from Australia. All reports are from Triassic rocks which are much older than the Kumbarilla Beds at Chinchilla. Solely on the basis of its ovule structure *Dawesia* has previously been assigned tentatively to the Peltaspermales by Clifford and Carney (1994). However,the cupulate infructescence of *Dawesia* makes it unlikely that the genus is a peltasperm, the ovules of which are borne on the lower surface of umbrella-like discs. The Corystospermales are also unlikely to be relatives of *Dawesia* because although their ovules are borne in cupules these are uniovulate and the apices of the ovules are curved and bifid.

The cupules of *Petriella* like those of *Dawesia* are embedded in permineralised peat but are much better preserved notwithstanding their Triassic age. Although *Petriella* has multiovulate cupules these differ markedly from those of Dawesia in being much smaller, and the ovules are triangular instead of circular in transverse section with the integument forming a distinct tube about the micropyle (Taylor et al., 1994). Accordingly, the two genera cannot be regarded as closely related on the basis of their cupule and ovule morphologies.

Therefore, until further evidence is available, it is appropriate that *Dawesia* be placed in a unique Order of uncertain affinity.

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